Great Basin Naturalist 53(1), pp. 48-58

CRYPTOGAMS, VASCULAR PLANTS, AND SOIL HYDROLOGICAL RELATIONS: SOME PRELIMINARY RESULTS FROM THE SEMIARID WOODLANDS OF EASTERN AUSTRALIA

D. J. Eldridge[1]

ABSTRACT.—Grazed and ungrazed sites were examined in a semiarid woodland in eastern Australia to determine relationships within various types of cryptogams, and the role of cryptogams in pasture dynamics, infiltration, and water erosion. Strong relationships were found between vascular plant cover and cover of cryptogams for nine rangeland sites over an 18-month period. In the absence of vascular plants, sites with low cover of cryptogams were dominated by algae. The presence of a cryptogamic crust had no significant effect on infiltration at ungrazed sites but significantly increased infiltration at some grazed sites. Splash erosion was very low on soils with at least 50% cryptogam cover. Below this level splash erosion increased markedly along with the proportion of fine sediments lost.

Key words: cryptogamic crusts; hydrology, soil; infiltration; cryptogam dynamics; microphytic crusts; semiarid woodlands; sorptivity; Australia.

Cryptogamic or microphytic soil crusts are an important component of arid and semiarid rangeland environments. They occur as assemblages of algae, lichens, liverworts, and mosses and, in some areas where vascular plants are absent, are the predominant biological ground cover. In these environments cryptogams play an important role in soil stability, nitrogen fixation, and biomass production (Isichei 1990).

Cryptogams are commonly pioneering species in the revegetation of degraded soils (Bailey et al. 1973). Observations in some areas in semiarid eastern Australia suggest that cyanobacteria are the most common taxa found on disturbed sites. The relationship between vascular flora and cryptogams, however, is not well understood. From studies in North America, Schofield (1985) concluded that mosses increase in cover as forbs and grasses are progressively eliminated by overgrazing. Studies in the semiarid woodlands of eastern Australia (Mucher et al. 1988) reported a strong positive relationship between vascular plant biomass and the area of the soil surface covered by cryptogamic mats.

The role of cryptogams in infiltration is not well understood and results of reported research have often been conflicting. Increased infiltration has been observed on areas with microphytic crusts compared to areas without (e.g., Blackburn 1975, Fletcher and Martin 1948, Gifford 1972, Yair 1990). However, other researchers (e.g., Brotherson and Rushforth 1983, Danin 1978, Graetz and Tongway 1986, Loope and Gifford 1972, Rogers 1977) showed that the presence of cryptogams of variable cover reduces infiltration.

As cryptogams are often associated with sparsely vegetated landscapes with high natural rates of erosion, it is natural to assume that they play a role in reducing erosion (West 1990). Claims of reduced water erosion due to cryptogamic crusts are widely reported in the literature (e.g., Campbell et al. 1989, Chartres and Mucher 1989, Greene et al. 1990, Kinnell et al. 1990, Mucher et al. 1988, Rushforth and Brotherson 1982, Yair 1990). The resistance of cryptogamic crusts to erosion is thought to be due to cyanobacteria and to a lesser extent fungi associated with the cryptogamic mats. Polysaccharides produced by cyanobacteria and fungal hyphae (Tisdall and Oades 1982) bind their cells, filaments, and surrounding soil particles into small aggregates (Shields and Durrell 1964). These aggregates have enhanced stability in water and help to protect the soil from wind

---

[1] [illegible] Management, [illegible] NSW [illegible] Australia. Present address: Graduate School of the Environment, [illegible]

and water erosion (Fletcher and Martin 1948, Greene and Tongway 1989).

The role of cryptogams in ecological processes in semiarid regions has received little attention until recent reviews by Harper and Marble (1988) and West (1990) appeared in the literature. These reviews draw heavily on published research from semiarid regions of North America, Australia, and Israel. In the semiarid rangelands of eastern Australia, research is currently underway to examine the spatial distribution of cryptogamic surfaces, their relationship to vascular plants and rangeland condition and trend, and their effects on infiltration and erosion.

In this paper I present preliminary results of research on the distribution of cryptogamic flora and their role in vascular plant dynamics, splash erosion, and infiltration.

MATERIALS AND METHODS

Study Area

All studies were undertaken at Yathong Nature Reserve and 'Coan Downs', approximately 140 km southwest of Cobar in western New South Wales, Australia (32°56′S, 145°35′E, Fig. 1). Sheep grazing on native pasture is the principal land use in the region. 'Coan Downs' is typical of grazing properties in the area where merino ewes and wethers are run in paddocks of approximately 2000–4000 ha. Yathong Nature Reserve has not been grazed by sheep, however, since 1977. It currently carries large populations of rabbits (*Oryctolagus cuniculus*), grey and red kangaroos (*Macropus giganteus*, *M. fuliginosus*, and *M. rufus*), and feral goats (*Capra hircus*; Leigh et al. 1989).

The climate of the area is characterized by a low and unreliable rainfall averaging 350 mm per annum. Rainfall is evenly distributed throughout the year, although winter rainfall (June–August) is slightly less variable than summer rainfall. Maximum and minimum diurnal temperatures range from 35.0°C and 19.6°C in January to 16.0°C and 3.6°C in July. The area receives on average 23 frost days per annum, and annual evaporation at Cobar to the north of the study area is approximately 2575 mm (Bureau of Meterorology 1961). The highest wind runs are experienced from spring and late summer (September–February), which correspond with the period of maximum soil erodibility.

Fig. 1. Location of the study area in eastern Australia.

Yathong Nature Reserve and 'Coan Downs' are located on the southern tip of the Cobar Pediplain on gently undulating plains to 3% slope derived from Paleozoic rocks including granites (Iwaszkiewicz and Semple 1988). The soils overlying much of this landscape are red and red-brown clay loams and loams (Typic Haplargids; Soil Survey Staff 1975), with gradational texture profiles containing variable amounts of stone and gravel.

Vegetation at Yathong Nature Reserve and 'Coan Downs' is open woodland dominated by red box (*Eucalyptus intertexta*), white cypress pine (*Callitris glaucophylla*), and wilga (*Geijera parviflora*). Understory pastures are dominated by speargrasses (*Stipa* spp.), wiregrasses (*Aristida* spp.), and various annual forbs.

Cryptogam Dynamics Study

In conjunction with the study of the role of cryptogams in infiltration (discussed below), data were collected on total cover of cryptogams and cover of various cryptogam types (i.e., mosses, algae, lichens, and liverworts). Data are presented for 43 locations from the ungrazed Yathong Nature Reserve and 34 locations from the grazed 'Coan Downs'.

Pasture Dynamics Study

As part of a larger study of the temporal changes in pasture dynamics, cover and species composition of vascular plants and cover of cryptogams were recorded at regular intervals from nine large sites between September 1988 and February 1990. Each site measured 500 × 500 m. At each site, fifty 0.25-m^2 quadrats were systematically sampled and the following components measured: cover of perennial grasses, ephemerals, bare soil, litter and cryptogams, and total aboveground biomass of pasture. For the purpose of this study individual cryptogamic taxa have been pooled.

Infiltration Study

At Yathong Nature Reserve and 'Coan Downs', two sites were selected (independent of the nine pasture dynamics sites above) for investigating the role of cryptogam cover on two infiltration parameters: sorptivity (mm h$^{-0.5}$) and steady-state infiltration (mm h^{-1}).

Sorptivity is the initial rapid phase of infiltration, usually lasting less than 10 min, which is dominated by capillary forces. Steady-state infiltration, however, occurs during the latter stages of infiltration when only gravitational forces predominate. Steady-state infiltration is strongly related to soil porosity, which in turn depends on type and amount of cover.

At Yathong Nature Reserve, where soil surface and vegetation cover are in excellent condition, 44 locations were selected for infiltration measurements, i.e., 22 each for sorptivity and steady-state infiltration. At 'Coan Downs', unlike Yathong Nature Reserve, historical overgrazing has lead to the development of distinct zones of erosion and deposition known as production and sink zones, respectively. These commonly occur in landscapes where fluvial processes predominate. Together with an intermediate transfer zone, which has characteristics of both production and sink zones, these zones constitute what are known as erosion cells (Pickup 1985). At 'Coan Downs' 10 and 7 locations were selected for measurements of sorptivity in the production and sink zones, respectively, and 9 and 7 locations for measurement of steady-state infiltration in the two zones, respectively.

Locations for detailed measurements of sorptivity and steady-state infiltration were selected so that the soil surface under the base of the permeameter (diam = 21.2 cm) varied in cryptogam cover from 0 to 100%. Only areas in which cryptogam cover was evenly distributed under the permeameters were selected. I avoided choosing locations such as the boundary of completely bare and completely covered areas, which theoretically might have represented a mean cover of 50%. Before detailed infiltration measurements were taken, total cover of cryptogams and relative contribution by various cryptogam types (i.e., lichens, mosses, algae, liverworts) were visually estimated, and color slides of each plot were taken to calibrate field estimates of total cover.

Sorptivity and steady-state infiltration were measured under ponded conditions, i.e., under a permanent pond of 10 mm of water. The ponded permeameter measures infiltration through all soil pores, i.e., matrix or small soil pores, and macropores (>0.75 mm in diameter), which are generally produced by roots and faunal activity. The ponded permeameter was placed on a steel ring that was gently tapped into the soil and sealed at the sides to prevent leakage. Infiltration runs were carried out until steady-state was achieved, usually within 30 min. Sorptivity and steady-state infiltration were calculated according to the method of White (1988).

Splash Erosion Study

Undisturbed cores of soil with associated cryptogams were collected from Yathong Nature Reserve by pushing 75-mm lengths of 90-mm-diameter PVC tubes into moist soil flush with the surface and excavating the intact tube. Cryptogam cover was estimated visually in the field by two observers prior to collection. One hundred thirty-five samples were collected representing five classes of cryptogam cover, i.e., completely bare (0%), 25%, 50%, 75%, and 100% cover. Cores were then transported to the laboratory, placed in a large tray beneath the simulator, and subjected to a simulated rainfall of 45 mm h^{-1} for 20 min. Each replicate consisted of nine cores in a three-by-three array under the simulator. Fifteen simulations (5 treatments × 3 replicates) were performed.

Runoff water and sediment were collected at the lower end of a collecting tray by using a vacuum pump at 2-min intervals. Sediment bulked across replicates was separated into five size classes: <0.0553 mm (silt and clay), 0.0553–0.0990 mm (very fine sand), 0.0991–0.2515 mm (fine sand), 0.2516–0.500 mm (medium sand), and >0.500 mm (coarse sand and a few aggregates) by gently washing through a nest of sieves.

Statistical Analyses

Simple regression and correlation analyses were used to examine the relationships between total cover and cover of various cryptogam types, cryptogam cover and vascular plant cover, and cryptogam cover and infiltration parameters.

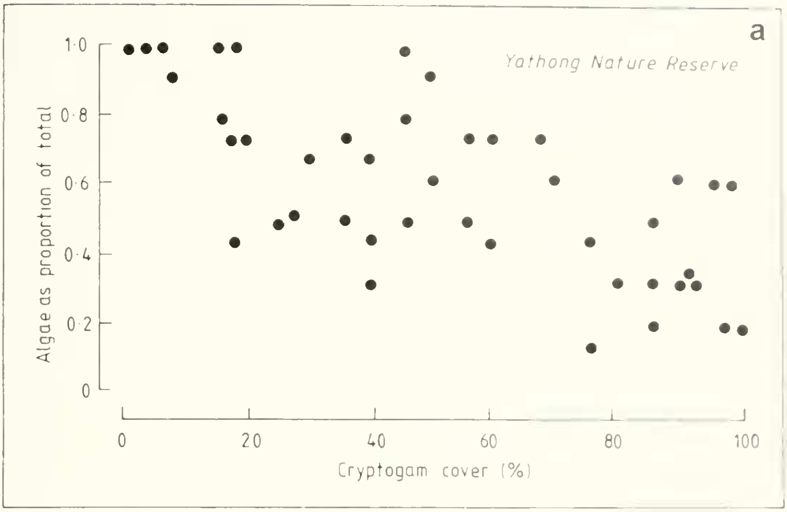

Fig. 2a. Relationship between cover of algae as a proportion of total cover and cryptogam cover (%) at Yathong Nature Reserve.

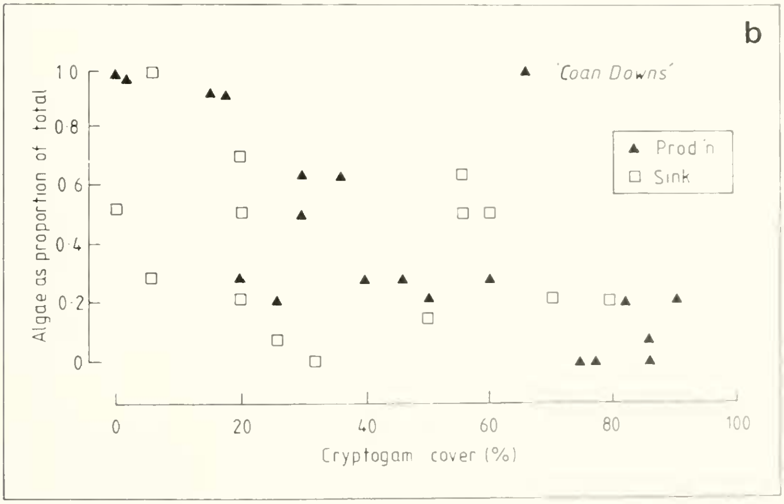

Fig. 2b. Relationship between cover of algae as a proportion of total cover and cryptogam cover (%) at 'Coan Downs'. Data are partitioned between the production and sink zones (see text for details).

Results are expressed as mean ± standard error of the mean (s.e.m.).

RESULTS

Cryptogam Dynamics

Sites with low total cover of cryptogams were dominated by algae, and, as cover increased, so did the relative contribution by mosses and some liverworts (Figs. 2a, 2b). Very few lichens were found at any location. When data were pooled across grazed and ungrazed sites, there was a significant negative correlation between total cryptogam cover and proportion of that cover comprising algae ($R^2 = .28$, $P < .001$, $n = 77$). Partitioning the data between grazed and ungrazed sites markedly increased the magnitude of the coefficients of determination for the ungrazed site ($R^2 = .45$, $P = .000$, $n = 43$) but only slightly for the grazed site ($R^2 = .30$, $P = .001$, $n = 34$). Neither the slopes nor intercepts

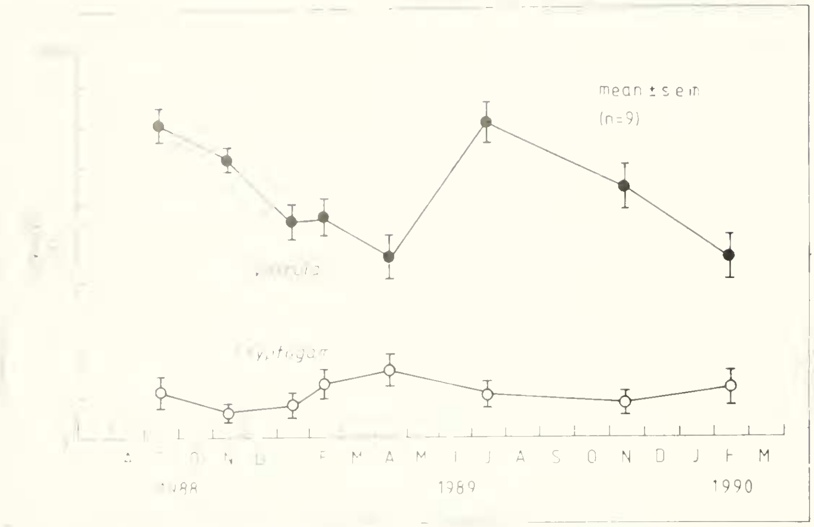

Fig. 3. Changes in cover (%) of cryptogams and vascular plants between September 1988 and February 1990.

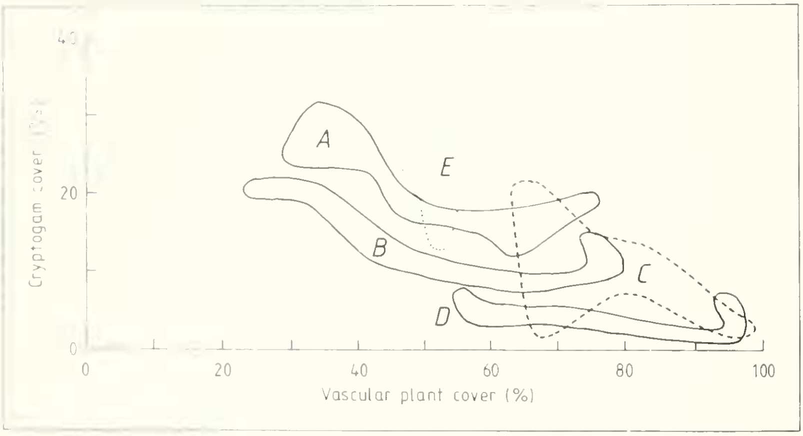

Fig. 4. Relationship between cryptogam cover (%) and vascular plant cover (%) for five groups of sites at Yathong Nature Reserve and Coan Downs. Clusters depict changes between the eight sample dates shown in Figure 3. A = sites dominated by winter-growing ephemerals (sites 1 & 2), B = sites dominated by winter-growing ephemerals and *Aristida* spp. (3 & 4), C = sites dominated by winter-growing ephemerals and *Stipa* spp. (7 & 8), D = gilgaid red earth sites dominated by summer-growing perennial grasses (5 & 6), and E = site dominated by mixed summer- and winter-growing perennial grasses (9) (see text for discussion of sites).

of the two relationships for the grazed or ungrazed sites were significantly different.

Correlations Between Cryptogams and Vascular Plants

Across the nine large sites, cryptogam cover ranged from 7.1% to 17.6%, and cover of vascular plants ranged from 45.7% to 80.1% (Fig. 3). Cryptogam cover was strongly negatively correlated with vascular plant biomass. Correlations [illegible] 0.65 at sites and times when biomass varied from 0.16 kg m^{-2} to 0.32 kg m^{-2}. Increasing biomass did not affect the magnitude nor the significance of the correlations between cryptogam cover and any of the independent variables. There was no evidence that high biomass levels were masking the presence of cryptogams on the soil surface. At all sites and times, cryptogam cover was negatively correlated with cover of litter, perennial grasses, and ephemerals and positively correlated with cover of bare soil.

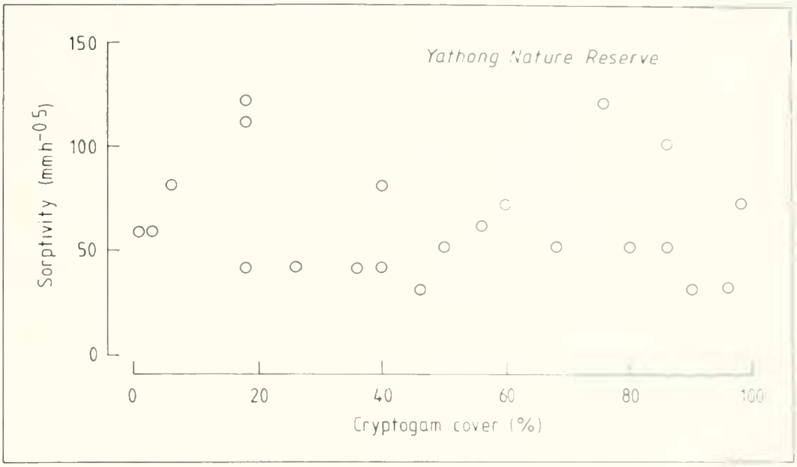

Fig. 5. Relationship between ponded sorptivity (mm h$^{-0.5}$) and cryptogam cover (%) at Yathong Nature Reserve

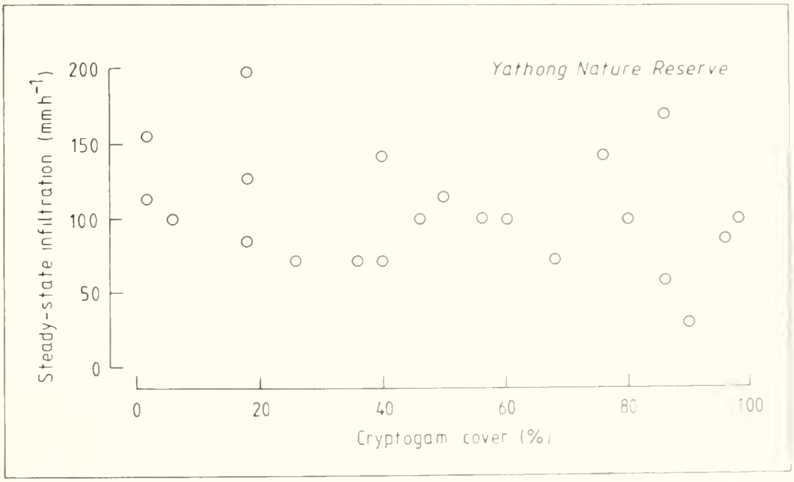

Fig. 6. Relationship between ponded steady-state infiltration (mm h^{-1}) and cryptogam cover (%) at Yathong Nature Reserve.

Temporal changes in cover of cryptogams and vascular plants varied between sites, with some sites fluctuating widely while others were more stable (Fig. 4). Perennial grass-dominant sites were generally the most stable. For example, there were only small changes in cryptogam cover on the gilgaid soils dominated by summer-growing perennial grasses (group D). Conversely, sites dominated by ephemerals (group A) experienced the largest fluctuations in cryptogam cover over time.

Infiltration

The relationship between cryptogam cover and the two infiltration parameters differed between grazed and ungrazed sites. At the ungrazed site at Yathong Nature Reserve sorptivity averaged 62.9 ± 5.84 mm h$^{-0.5}$ (range 28–118 mm h$^{-0.5}$), and steady-state infiltration averaged 103.6 ± 8.3 mm h^{-1} (range 25–199 mm h^{-1}). Sorptivity was independent of cryptogam cover ($R^2 = .0$, $P = .473$, $n = 22$, Fig. 5), and there was a slight though insignificant decrease

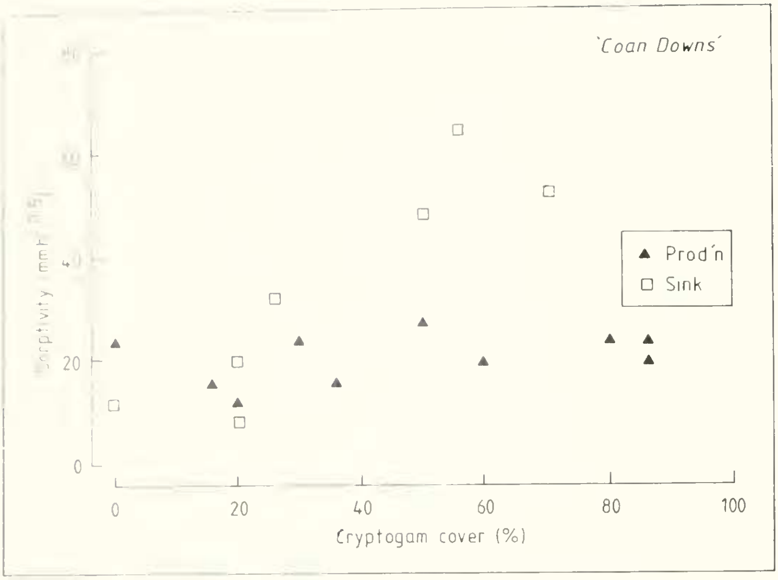

Fig. 7. Relationship between ponded sorptivity (mm h$^{-0.5}$) and cryptogam cover (%) at 'Coan Downs'. Data are partitioned between the production and sink zones.

in ponded steady-state infiltration with increasing cover (R^2 = .0, P = .20, n = 22; Fig. 6).

At the grazed 'Coan Downs' site, sorptivity averaged 28.1 ± 3.7 mm h$^{-0.5}$ (range 10–64 mm h$^{-0.5}$), and steady-state infiltration averaged 39.7 ± 5.5 mm h^{-1} (range 11–103 mm h^{-1}). The high degree of variability within any one cover class meant that at low cover levels sorptivity and infiltration were sometimes low but sometimes high and vice versa. Consequently, the general trends of increasing sorptivity and steady-state infiltration with increasing cover were not significant (P = .121 and .053, respectively).

To account for a greater proportion of the variation in sorptivity and steady-state infiltration data were partitioned between the production and sink zones, the two major geomorphic zones operating at the grazed site at 'Coan Downs' (see Methods).

There was a strong positive relationship between sorptivity and cryptogam cover at 'Coan Downs', which was significant in the sink zone (R^2 = .78, P = .007, n = 7) but not in the production zone (R^2 = .08, P = .225, n = 10; Fig. 7). Steady-state infiltration followed the same trend as sorptivity. There was a strong positive relationship between ponded infiltration and cryptogam cover [illegible] in the sink zone (R^2 = .84, P = [illegible], n = 7) but not in the production zone (R^2 = [illegible], P = [illegible]; Fig. 8).

Splash Erosion

Sediment removal increased significantly with decreases in cryptogam cover ($F_{4,10}$ = 45.8, P < .0001; Fig. 9). Little sediment was removed at cover levels >50%, but at lower levels than this, erosion increased markedly. The relationship between sediment removal and cryptogam cover was:

$$Y = e^{5.73-0.032c}$$

where Y is total sediment removal (g m^{-2}) and c is cryptogam cover (%). Cover of cryptogams explained 81% of the variation in sediment removal.

The rate of sediment removal varied among the five cover classes. Removal rates for the 100%, 75%, and 50% cover classes were very low and averaged 0.6, 2.0, and 3.2 g m^{-2} min^{-1}, respectively. The 25% and 0% cover classes, however, had a much higher rate of sediment removal (i.e., 8.8 and 15.3 g m^{-2} min^{-1}, respectively).

The particle-size distribution of eroded material was also influenced by cryptogam cover. As cover decreased, the proportion of silts, clays, and very fine sand increased and coarse sands decreased. Thus, not only was more sediment lost from soils with low cryptogam cover, but more of that sediment comprised silts and clays, onto which the majority of the nutrients are

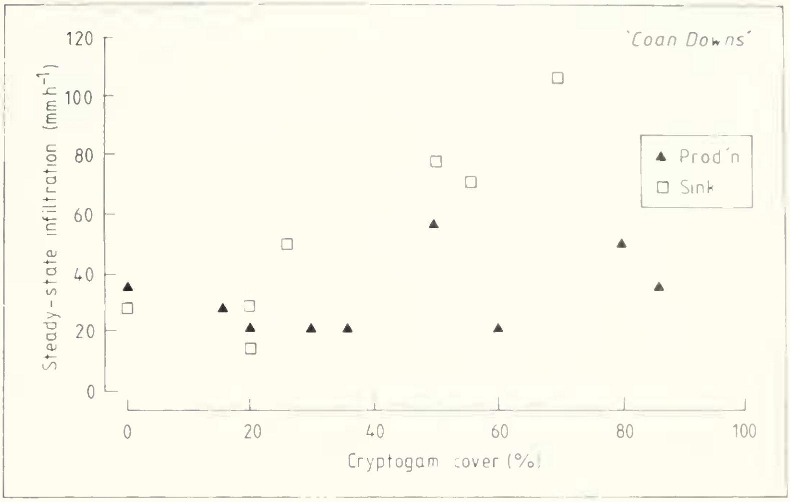

Fig. 8. Relationship between ponded steady-state infiltration (mm h^{-1}) and cryptogam cover (%) at 'Coan Downs'. Data are partitioned between the production and sink zones.

bound. Furthermore, much of the fine material was removed during the early stages of runoff; i.e., as simulations proceeded, a higher proportion of coarse particles was removed.

DISCUSSION

In the semiarid woodlands of eastern Australia, overgrazing by domestic and feral animals over the past 100 years has resulted in a severe depletion of the native pastures (Harrington et al. 1984) and a shift from desirable perennial grasses to less desirable perennials and ephemerals (Iwaszkiewicz and Semple 1988). This has been accompanied by reduced productive potential of the soil and increased bare soil, runoff, and soil erosion (Johns 1983). In this environment vascular plant cover is highly discontinuous or patchy, and cryptogams are often the only biological soil cover providing protection from erosion.

Cryptogam Dynamics

In this study, plots with a low cover of cryptogams were dominated by algae, and plots with a high cover by mosses and some lichens. This is not surprising inasmuch as algae act as pioneers in plant succession (Isichei 1990), and as the soil surface becomes more stable, mosses and lichens gradually increase in dominance (Dunne 1989) at the expense of algae. Because of this successional sequence in development of cryptogamic crusts from algae-dominant to moss-dominant and lichen-dominant, the presence of a surface dominated by mosses and lichens might be used as an indication of the stability of the soil surface. There is some evidence (Eldridge unpublished data) that the more stable sites at Yathong Nature Reserve and 'Coan Downs', i.e., those dominated by perennial grasses, had higher covers of moss and some lichen compared with the less stable ephemeral sites.

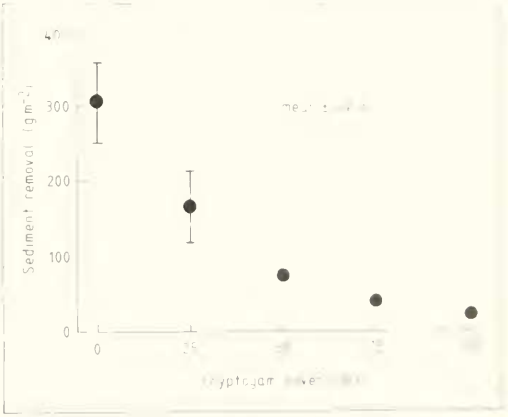

Fig. 9. Influence of cryptogam cover (%) on sediment removal (g m^{-2}) during 20 minutes of simulated rainfall. Symbols enclose standard errors of the mean except where shown (n = 3).

Cryptogams and Vascular Plants

In these studies decreases in vascular plant cover were associated with increases in the cover of cryptogams and vice versa (Fig. 4). Cryptogam cover was negatively correlated with plant biomass and cover of litter, perennial grasses, and ephemerals, and positively correlated with cover of bare ground. This is consistent with studies from the semiarid shrublands of South Australia where cryptogam cover increased as cover of herbs and trees decreased following long-term exclusion of grazing (Crisp 1975). Similarly, Schofield (1985) reported that grazing increased the relative cover of mosses by reducing the cover of vascular plants.

The interaction between vascular plants and cryptogams has been described as a 1:1 tradeoff (West 1990), where a decrease in the proportion of one component results in an increase in the other. Thus, management practices leading to a change in the cover of vascular plants would ultimately affect the cover of cryptogams. Given an increase in vascular plant cover through exclosure or destocking, it is likely that cryptogam cover would decrease through increased competition for light and moisture and through overtopping by perennial grasses (Looman 1964).

In marked contrast to my results, numerous studies have reported positive correlations between cryptogam cover and vascular plant cover. For example, Graetz and Tongway (1986) showed a significant positive correlation between the cover of perennial chenopod shrubs and cover of cryptogams, and Mucher et al. (1988) described how biomass of biennial grasses and forbs increased as cover of cryptogams increased. In the desert grassland in Utah Kleiner and Harper (1977) showed how species richness of vascular plants increases with richness of nonvascular flora. Similarly, in the western deserts of North America, extensive damage to the vascular plant community through trampling by cattle is associated with a considerable reduction in the nonvascular flora (J. Johansen personal communication).

The total cover of cryptogams on rangeland sites is generally (although not exclusively) regarded as an indicator of desirable range condition. More studies are needed, however, to [illegible] the development of a cryp[illegible] to the develop[illegible] crusts (West [illegible]

Infiltration

Although cryptogams have been reported as affecting infiltration, results from Yathong Nature Reserve and 'Coan Downs' indicate that other soil factors may be more influential. The positive linear relationship between cryptogam cover and infiltration on the grazed sites in this study is consistent with a few studies (Fletcher and Martin 1948, Gifford 1972) but is inconsistent with the bulk of published research suggesting that cryptogamic crusts reduce infiltration (see West 1990).

At Yathong Nature Reserve, where grazing by domestic animals ceased in 1977, there was a nonsignificant trend of decreasing infiltration with increasing cryptogam cover. The differences in response to changes in cryptogam cover may be explained in part by the differences in soil physical properties between the grazed and ungrazed soils. At a number of sites in Yathong Nature Reserve, Eldridge and Rothon (1992) found that changes in vascular plant cover explained very little of the variation in infiltration, runoff, and sediment yield. This is thought to be due to the high macroporosity status of the soil on the ungrazed sites, with infiltration determined by the overriding influence of soil physical properties.

On moderately degraded soil surfaces, a combination of a smooth soil surface with poorly developed microrelief and minimal obstruction from grass butts, stones, and litter creates a situation where there is little opportunity for runoff to enter the soil profile. This was certainly the case at 'Coan Downs' where soil physical properties were severely degraded, macroporosity was low, and the majority of infiltration was restricted to flow through the soil matrix and very small biopores. In this environment cryptogams probably have two principal effects. First, they provide a physical barrier on the soil surface, protecting the surface against raindrop impact and thereby ensuring that the existing low levels of structural stability are maintained. Second, as infiltration is predominantly through matrix pores, fungal hyphae in the cryptogams assist by maintaining the integrity of these pores so that small increases in cryptogam cover result in marked increases in infiltration (Figs. 6, 7).

Cryptogams are thought to impact upon the hydrological cycle by their direct effect on soil surface roughness. Cryptogamic crusts increase surface microrelief by cementing wind- and water-eroded fragments into cohesive units, producing a raised, roughened surface (Anderson et al. 1982). This increased surface roughness retards overland flow, allowing more time for infiltration and deposition to occur (Warren et al. 1986). However, direct measurement of the surface microrelief of some ungrazed soils at Yathong Nature Reserve showed that cryptogams are not consistently associated with rougher soil surfaces (Eldridge 1991).

Splash Erosion

The splash erosion studies reported here demonstrate that the presence of a cryptogamic crust significantly reduces splash erosion from a semiarid red earth soil. Soil surfaces with >75% cryptogam cover had very little erosion, while surfaces with 25% cover or less had erosion of at least an order of magnitude greater (Fig. 8).

Numerous studies (e.g., Chartres and Mucher 1989, Kinnell et al. 1990, Yair 1990) have shown the importance of cryptogam cover in reducing soil loss and erosion. Booth (1941) found that soil loss on soil with a cyanobacterial crust is 20 times less than that from the same soil with no crust. More recently Tchoupopnou (1989) showed that under simulated rainfall, cryptogam-covered surfaces reduce the distance over which splash soil particles are displaced.

Not only did surfaces with a low cover of cryptogams lose more soil during simulated rainfall, but more of that soil comprised silts and clays. Thus, the loss of fine material from the low cover plots probably represents a continual removal of nutrients from the low cover surfaces and, at least in the case of nitrogen, a possible decline in productivity. This compares with the high cryptogam cover soils where eroded material comprised mainly coarse-grained sands and some aggregates >0.500 mm in diameter. Mosses and algae bound some of the particles removed during the erosion process. Thus, erosion may be assisting the dispersal and deposition of these microphytic taxa within the landscape.

As this study used small cores taken from the field, it is not possible to assess the degree to which splashed sediment is redeposited within the landscape. The soil loss values reported here probably overestimate what happens in the field where litter and plant butts would trap some moving sediment.

Conclusions

This study showed that cryptogams play a major role in infiltration and erosion in the semiarid woodlands of eastern Australia. Furthermore, strong relationships exist within cryptogamic taxa, and between cryptogam cover and cover and biomass of vascular plants.

At Yathong Nature Reserve and 'Coan Downs', the presence of cryptogams on the soil surface had a variable influence on infiltrating water but significantly reduced the susceptibility of the soil to splash erosion. Infiltration at the grazed sites at 'Coan Downs' was markedly different from that at the ungrazed Yathong Nature Reserve, probably a result of differences in soil physical properties, particularly macroporosity.

Under simulated rainfall, surfaces supporting a high cover of cryptogams were more stable and less erodible than surfaces with low cryptogam cover. Erosion from cryptogamic surfaces of varying cover probably results in a transfer of fine material and nutrients from areas of low cover to areas of high cover. Ultimately, low cover areas become less accessible to establishment by seedlings of vascular plants. Furthermore, the role of cryptogams in soil stability is enhanced during drought periods when cover of the usual vascular plant is either absent or severely reduced.

Acknowledgments

I thank John Pickard and Jeff Johansen for comments on earlier drafts of the manuscript and numerous colleagues for assistance with fieldwork. I am grateful to the Cullen-Ward family of 'Coan Downs' for allowing access to their property. The work was partially funded by the National Soil Conservation Programme of the Commonwealth Government of Australia under a permit from the NSW National Parks and Wildlife Service.

Literature Cited

Anderson, D. C., K. T. Harper, and R. C. Holmgren. 1982. Factors influencing development of cryptogamic soil crusts in Utah deserts. Journal of Range Management 35: 180–185.

Bailey, D., A. P. Mazurak, and J. R. Rosowski. 1973. Aggregation of soil particles by algae. Journal of Phycology 9: 99–101.

Blackburn, W. H. 1975. Factors influencing infiltration rate and sediment production of semiarid rangelands in Nevada. Water Resources Research 11: 929–937.

Booth, W. E. 1941. Algae as pioneers in plant succession and their importance in erosion control. Ecology 22: 38–46.

Brotherson, J. D., and S. R. Rushforth. 1983. Influence of cryptogamic crusts on moisture relationships of soils in Navajo National Monument, Arizona. Great Basin Naturalist 43: 73–78.

Bureau of Meteorology. 1961. Selected tables of Australian rainfall and related data. Bureau of Meteorology, Melbourne, Victoria, Australia.

Campbell, S. E., J. S. Seeler, and S. Golubic. 1989. Desert crust formation and soil stabilization. Arid Soil Research and Rehabilitation 3: 217–228.

Chartres, C. J., and H. J. Mucher. 1989. The response of burnt and unburnt rangeland soil surfaces to simulated raindrop impact and water erosion. Earth Surface Processes and Landforms 14: 407–417.

Crisp, M. D. 1975. Long-term changes in arid vegetation at Koonamore, South Australia. Doctoral dissertation, University of South Australia, Adelaide. 373 pp.

Danin, A. 1978. Plant species diversity and plant succession in a sandy area in the northern Negev. Flora 167: 409–422.

Dunne, J. 1989. Cryptogamic crusts in arid ecosystems. Rangelands 11: 180–182.

Eldridge, D. J. 1991. An evaluation of cover type as a predictor of soil surface roughness in a semi-arid grassland. Rangeland Journal 13: 61–66.

Eldridge, D. J., and J. Rothon. 1992. Runoff and sediment production from a semi-arid woodland in eastern Australia. I. The effect of pasture type. Rangeland Journal 14: 26–39.

Fletcher, J. E., and W. P. Martin. 1948. Some effects of algae and molds in the rain-crust of desert soils. Ecology 29: 95–100.

Gifford, G. F. 1972. Infiltration rate and sediment production on a ploughed big sagebrush site. Journal of Range Management 25: 53–55.

Graetz, R. D., and D. J. Tongway. 1986. Influence of grazing management on vegetation, soil structure and nutrient distribution and the infiltration of applied rainfall in a semi-arid chenopod shrubland. Australian Journal of Ecology 11: 347–360.

Greene, R. S. B., C. J. Chartres, and K. H. Hodgkinson. 1990. The effect of fire on the soil in a degraded semi-arid woodland. I. Physical and micromorphological properties. Australian Journal of Soil Research 28: [illegible]

Greene, R. S. B., and D. J. Tongway. 1989. The significance of (surface) physical and chemical properties in determining soil surface condition of red-earths in rangelands. Australian Journal of Soil Research 27: [illegible]

[illegible] 1988. A [illegible] for [illegible] [illegible] and [illegible] rangelands. [illegible] Application [illegible] management [illegible] Australia.

[illegible] M. D. [illegible] [illegible] Australia.

[illegible] Arid Soil Research and Rehabilitation [illegible]

[illegible]

ciated rangelands of western New South Wales. Technical Report No. 6, Soil Conservation Service of New South Wales.

Johns, G. G. 1983. Runoff and soil loss in a semi-arid shrub invaded poplar box (*Eucalyptus populnea*) woodland. Australian Rangeland Journal 5: 3–12.

Kinnell, P. I. A., C. J. Chartres, and C. L. Watson. 1990. The effect of fire on the soil in a degraded semi-arid woodland. II. Susceptibility of the soil to erosion by shallow rain-impacted flow. Australian Journal of Soil Research 28: 779–794.

Kleiner, E. F., and K. T. Harper. 1977. Soil properties in relation to cryptogamic ground cover in Canyonlands National Park. Journal of Range Management 30: 202–205.

Leigh, J. H., D. H. Wood, M. D. Holgate, A. Slee, and M. G. Stanger. 1989. Effects of rabbit and kangaroo grazing on two semi-arid grassland communities in central-western New South Wales. Australian Journal of Botany 37: 375–96.

Looman, J. 1964. Ecology of lichen and bryophyte communities in Saskatchewan. Ecology 45: 481–491.

Loope, W. L., and G. F. Gifford. 1972. Influence of a soil microfloral crust on select properties of soils under pinyon-juniper in southeastern Utah. Journal of Soil and Water Conservation 27: 164–167.

Mucher, H. J., C. J. Chartres, D. J. Tongway, and R. S. B. Greene. 1988. Micromorphology and significance of the surface crusts of soils in rangelands near Cobar, Australia. Geoderma 42: 227–244.

Pickup, G. 1985. The erosion cell—a geomorphic approach to landscape classification in range assessment. Australian Rangeland Journal 7: 114–121.

Rogers, R. W. 1977. Lichens of hot arid and semi-arid land. Pages 211–252 *in* M. R. D. Steward ed., Lichen ecology. Elsevier Press, Oxford.

Rushforth, S. R., and J. D. Brotherson. 1982. Cryptogamic soil crusts in the deserts of North America. American Biology Teacher 44: 472–475.

Schofield, W. B. 1985. Introduction to bryology. Macmillan, New York. 431 pp.

Soil Survey Staff. 1975. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. USDA Agricultural Handbook No. 436. Government Printing Office, Washington, D.C.

Shields, L. M., and L. W. Durrell. 1964. Algae in relation to soil fertility. Botanical Review 30: 92–128.

Tchoupopnou, E. 1989. Splash from microphytic soil crusts following simulated rain. Unpublished master's thesis, Utah State University, Logan.

Tisdall, J. M., and J. M. Oades. 1982. Organic matter and water-stable aggregates in soils. Journal of Soil Science 33: 141–163.

Warren, S. D., T. L. Thurow, W. H. Blackburn, and N. E. Garza. 1986. The influence of livestock trampling under intensive rotation grazing on soil hydrologic characteristics. Journal of Range Management 39: 391–395.

West, N. E. 1990. Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. Advances in Ecological Research 20: 179–223.

White, I. 1988. Tillage practices and soil hydraulic properties: Why quantify the obvious? Pages 87–126 *in* J. Loveday, ed., National soils conference review papers. Australian Society of Soil Science, Canberra, Australia.

Yair, A. 1990. Runoff generation in a sandy area—the Nizzana Sands, western Negev, Israel. Earth Surface Processes and Landforms 15: 597–609.